

MAMMALIAN ORGANIZATIONAL SYSTEMS

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ABSTRACT: Confusion exists concerning the relationship between the seemingly separate concepts of territory and hierarchy as used in describing mammalian organizational systems. This paper is an attempt to synthesize knowledge of these concepts into a single, continuous system of behavioral and ecological adaptations based on two ultimate factors that are characteristics of mammals, aggression and site attachment. Organizational systems result from the interaction of these characters and are further refined by proximate factors in mammalian life which include morphological, behavioral, and ecological adaptations.

In order to emphasize diversity of organizational systems, within and between species, and in order to clarify relationships between the concepts of territory and hierarchy, a possible classification of systems is suggested. Based primarily on individual and group organization, each of these two types is further elaborated into subtypes which are then defined, discussed, and illustrated.

INTRODUCTION

The conspecific relationships and interactions between individual mammals and the relationship of individuals to the land about them have long been subjects of interest, speculation, and research. Observations of such interactions have resulted in the development of two concepts of organization; hierarchies of one type or another, and territories, also of several types. Although earlier papers have pointed out the fact (Collias, 1944), it has become increasingly clear recently that these two concepts are not mutually exclusive. In the detailed studies of social behavior and population dynamics now being undertaken, it has frequently become difficult to assign a particular hierarchy type or territory type to a species. The tendency has been to treat the concepts independently in spite of assertions over the years that the two systems are quite related (*e.g.*, Darling, 1937; Godfrey and Crowcroft, 1960; Davis, 1958, 1966). Also, the tendency has been to treat the two concepts as causes rather than results, that mammals and their behavioral and spatial responses result from the type of social system, rather than that the social system is a product of the characteristics of the species and its environment. Consequently, there is considerable misuse and overuse of the terms without recognition that the concepts could be ill-defined and confused.

In 1957, Emlen cautioned against too rigid a definition of territory. Bourlière (1954, 1964) maintained that there was a link between the two ideas, hierarchy and territory, but that this link remained to be analyzed. Davis (1958) suggested that territory and dominance could be poles of a continuum.

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Eisenberg (1965) took a significant step in the direction of correlating the concepts of hierarchy and territory in his monograph on social organizations of mammals. He also emphasized the importance of many environmental factors which are involved in the determination of social organization of a species. Brown (1966) stated that adjustments of the Burt (1943) concept concerning home range and territory had become necessary. He considered that most mammals were actually part of an organized community rather than being singly organized on the basis of a utilized area (home range), part or all of which may be defended against conspecifics (territory). The best clear correlation of the two concepts in a general discussion was by Collias (1944). More recently Marler and Hamilton (1966) approached the problem by defining territory as the external reference for dominance fixed in space (see Marler and Hamilton for further references), a definition closely following Carpenter's (1958) concept of territory as a behavioral system expressed in a spatial-temporal frame of reference. Additional discussion of the problem by Marler and Hamilton included the concept of "individual distance" (Hediger, 1950) and the various types of dominance hierarchies. "Philopatry" (site attachment) (Mayr, 1963) and mutual avoidance were mentioned, with the implication that the two characteristics may be involved in the maintenance of home range. Earlier, Scott (1956) had discussed various ways of classifying behavior patterns and social relationships but did not cover in detail the problem as defined here.

Difficulty arises in attempting to define the term "territory." Mammalogists have traditionally followed the concept as outlined by Burt (1943, 1949), who essentially adapted the earlier ideas of Howard (1920) and other ornithologists to mammals. Use of the definition of Noble (1939) that a territory is "any defended area" has caused many workers to conceive of the social systems of many mammals as systems of overt (and occasionally covert) defense of a plot of ground, although some authors have realized that defense may not always be in regard to space (*e.g.*, Balph and Stokes, 1963). Noble himself had a much broader concept of territory and social dominance than this restrictive definition suggests. Live trapping studies of mammals abound in the attempt to fit uncertain data into a "territorial" system. Since many mammal species do not fit this definition, confusion occurs as to just what a territory is and what the limits of the concept may be. Jewell (1966) has recently discussed some problems with regard to the confusion of the concepts of territory and home range, including "core area" of Kaufmann (1962), "foci of activity" of Carpenter (1940), and "exclusive area" (undefended area) of Pitelka (1959), and has suggested that a further term, the "monopolized zone," be used. Also, Willis (1967) in his discussion of territory has considered the concept as one of "dominance reversal," that is, dominance in space decreases from the "center" to the periphery of the range of one individual, whereas dominance increases for an adjacent individual as the "center" of its range is approached.

Hierarchies and territorial systems are not mutually exclusive concepts relating on one hand to sociality and on the other hand to spatial utilization. Rather, these two concepts are actually the possible resultant extremes in the evolution of mammalian organizational systems, with many possible intermediate types of systems employing varying degrees of spatial territory and social hierarchy formation. Territory and hierarchy are not different in kind but rather in degree. Tinbergen (1957) and others have recognized that there are territories of space which "move" with the traveling individual, that is, there is defense of a space but this may change from hour to hour, week to week. Furthermore, several workers have found that there are hierarchy systems within territory systems (Brown, 1966; Crowcroft, 1955; Davis, 1958; Reimer and Petras, 1967) and that at high population densities normally territorial species may become hierarchical.

The purpose of this paper is to suggest a classification which may provide a framework which will encompass the data accumulated and still accumulating on the organizational systems of mammals from both spatial and behavioral concepts. Eisenberg (1965) has classified mammalian social systems on the basis of two categories, solitary and communal, with the latter divisible into subunits, the largest of which is the family band, and has extended this with a detailed discussion of the concepts for rodents (Eisenberg, 1967). I propose here to utilize current terminology of a broader scope, with some additions, in an overlay of the work of Eisenberg and of the concepts of hierarchy and territory as discussed in Collias (1944) and in Marler and Hamilton (1966). This classification is, then, neither ecological nor behavioral but rather, hopefully, a synthesis of the two areas into a unified concept of the structure of mammalian organizational systems.

ULTIMATE FACTORS IN ORGANIZATIONAL SYSTEM FORMATION

Hierarchies, territories, and the spectrum in between are different means of expression of the same characteristics of mammals. Bourlière (1954, 1964) has stated that hierarchy and territory formation are both "manifestations of aggressiveness within the species," and Eisenberg (1965) stated that territory, individual distance, harem formation, and hierarchy formation were all implemented by aggressive behavior. Tinbergen (1957) has expressed the idea that territory is a result of two distinct tendencies which may or may not occur together, namely, site attachment and intraspecific hostility. Eisenberg (1965), although particularly stressing aggression, also mentioned site attachment as a factor. Marler and Hamilton (1966) alluded to both aggression and site attachment as being involved in animal spacing. I should like to extend these two concepts, site attachment and aggression, separately and together, and state that all mammalian organizational systems depend ultimately on these two characteristics.

Denial of the existence of site attachment as a mammalian characteristic is difficult. Innumerable studies are familiar to mammalogists, both trap-mark-

release and visual observation, which attest to the frequency with which individual mammals remain in the same area for long periods of time. This fact has been conceptualized by Burt (1943) in the idea of "home range." True, there may be some home range shifting, but apparently few mammal species are nomadic with no fixed home area. The advantages of and preferences for such specific places have been discussed by Darling (1937). Furthermore, the now well-known tendency for many mammals to home over surprisingly long distances lends additional support to the idea that attachment to a specific site is a fundamental character for most mammals. The "desire" for the security of a familiar area is apparently very strong.

Aggressive tendencies are more difficult to assess, perhaps because they are noticeable primarily as avoidance. It seems clear, however, that aggression does exist in most mammals. Aggression is defined in many ways, but here refers to the antagonistic reactions of individuals which are operative at high intensity (attack) to those reactions just to, but not including, complete passivity. Defense, therefore, is included within this definition of aggression. Such actions are directed at conspecifics for the attainment of some specified goal such as a nest site, food, sex, or psychological well-being. This may be overt ("face to face") or covert (chemical, etc.). Discussion concerning aggression does not appear to question whether it is present but whether it is innate or learned (see Carthy and Ebling, 1964; Dobzhansky, 1967). It is not important here to discuss this particular controversy but merely to point out that aggression is a part of the make-up of most mammals, whether innate or learned during the maturation process.

Site attachment and aggression, then, form two basic powerful tendencies which help dictate how a mammal will respond to its environment, even though the environment may also be influencing these two characteristics in the individual, through selection.

PROXIMATE FACTORS IN ORGANIZATIONAL SYSTEM FORMATION

The actual form assumed by an organizational system will depend on several factors additional to site attachment and aggression. These systems must be adaptive, that is, they should be the best system devisable in order to insure survival for the species, and they must be sufficiently flexible to allow short-term adjustments of the system as the environment dictates. Proximate factors form the natural selective processes which mold a population into the proper organizational system for any particular species under its current environmental conditions.

The proximate factors listed in this paper undoubtedly are not all of those involved, nor are they listed in any particular order of importance. Assessment of the importance of these, and other factors, must be made for each individual species studied. For further discussion of several of these factors, I refer the reader to the work of Eisenberg (1965).

1. Basic morphology—The physical capabilities of a species in the utili-

zation of a habitat are involved in the type of social system developed. A mouse does not cover as much ground in its daily routine as does a deer, so the likelihood of similar organizational system development is remote. Furthermore, the very conspicuousness of the deer as opposed to the mouse will have an effect on the type of system that will develop.

2. Level of aggressive tendency—Some species are more aggressive than others, although factors controlling the level of aggression are poorly known.

3. Level of site attachment—Attachment to a particular area may be very strong in some species and individuals or it may be relatively weak.

4. Habitat occupied—Crook (1966) stressed habitat differences as being responsible for social system differences between the baboons *Theropithecus gelada* and *Papio cynocephalus*. Also, many grassland dwellers have developed systems different from those of forest dwellers of comparable size.

5. Surrounding mammal populations—Interspecific reactions and interactions may influence the organizational system developed. A special case of interspecific interaction, and perhaps the most important, is the predator-prey relationship. The predator species requires a different type of organization than does its prey and one may influence the type of system that the other evolves (Estes, 1966). A further possible influence is that of biological rank (Hediger, 1950) in which there may be a "hierarchy" among individuals of different species, or where one species may be dominant over another (also see MacMillen, 1964, and especially Calhoun, 1963).

6. Availability of nest, den, and refuge sites—If nest sites, etc., are readily available and numerous, there will be little or no competition for them. However, if the population density increases, or sites are destroyed, thereby leaving such sites in short supply, there may be increased aggression, causing a different organizational system to develop, at least until the situation is relieved.

7. Availability and kinds of food—The comments in number 6 also apply here. In addition, the organizational system may be influenced by food type. Eisenberg (1965) has emphasized the similarity of the social systems of the various anteaters (Myrmecophagidae, Manidae, Orycteropodidae).

8. Reproductive requirements—Many conditions must be met here, but the most important factors are, first, getting the sexes together, and, second, caring for the young. There are numerous examples of organizational systems which differ between the breeding and non-breeding seasons, and the method of care of the young may vastly influence the organizational system (for example, altricial versus precocial, and male participation in care).

9. Differential niche utilization by the sexes (or age groups)—Recent evidence has indicated that there is a partitioning of the habitat by the sexes in some birds (Selander, 1966). Future research will certainly show that such partitioning also occurs in mammals, particularly in those with great sexual size dimorphism.

10. Population density—There is now evidence that territorial systems

may become hierarchical systems with increased population density, and vice versa (Brown, 1966, and others). A hierarchy allows a greater number of animals to occupy a given area than does a territorial system. Selection here for flexibility of organizational systems is evident.

11. Climate—Difficult weather conditions and climates can alter the system employed, either on a temporary basis (aggregation at food or water sources during severe winters or droughts) or from a long-term evolutionary standpoint.

THE EFFECT OF PROXIMATE FACTORS

General examples

Two examples will illustrate how proximate factors impinge upon a population in order to form a particular type of organizational system.

The northern fur seal (*Callorhinus ursinus*) is a species of mammal adapted for an aquatic life, but it must return to land to breed. Site attachment is high as is evidenced by return to the same localities, even to the natal site in females, to breed and bear young (Kenyon, 1960). These are large, conspicuous animals needing little cover while on land since land-based predators are essentially non-existent. Food on land is not a factor as they are dependent upon the sea. Aggressive level is high among bulls, less so among females. The population density at the restricted breeding site is high, hence spatial territory is not possible for all individuals. As a consequence, a system of male dominance and harem formation has evolved. Because of the aggression of the dominant bulls, younger and weaker bulls are forced to exist in bachelor herds.

The second example will be drawn from a completely different physical type, a small mouse. Mobility is not great, that is, not much space can be covered by the individual in a day, or even, for the most part, in a lifetime. The habitat occupied contains other species competing for the same things, food, nest sites, etc. Cover may be good, but aggregations as a normal way of life are inadequate as predators could easily decimate the population (note the predation on lemmings during their "explosions"). Thus, any social system involving harems or large aggregations would not be adaptive. Rather, it is more effective to spread the individuals out over much of the available habitat, each defending its own small area, its nest site, or perhaps just itself or the area immediately around it (psychic space).

Sex in relation to other proximate factors

Organizational systems may be reproductive, non-reproductive, or both. It is well-known that many species of mammals achieve a specific type of system during the breeding season, whereas they exhibit another during the non-breeding period (e.g., many ungulates), or are apparently "unorganized" during non-reproductive phases (e.g., some rodents, eared seals). Others maintain a similar sort of system whether breeding or non-breeding (e.g., many

primates, some rodents). Also, according to Eisenberg (1965), there is a "social drive" distinct from sexuality and parental care. It is apparent, then, that organizational systems are not based entirely on sex. Site attachment is a year around phenomenon. Even individuals of migratory species tend to return to the same sites at each end of the migratory path. Habitat selection, and other proximate factors of organizational system formation, are also in effect all year. Sex, however, is usually a seasonal phenomenon and the intricate systems that must be developed for the perpetuation of the species through the more frequent breeding of the better adapted individuals should be regarded as organizational systems superimposed on the regular, normal system dictated by other environmental factors. The sexual hierarchy or territory is apparently a device evolved to insure the most efficient and bio-energetically economical way of perpetuating the species under its current environmental conditions, while at the same time meeting the basic requirements of the species with regard to psychological and physical well-being. Sexual systems are superimposed upon the basic system of the species for that particular habitat (with possible slight differences for variations of the habitat), whether this be a loose society (non-regimented in the sense of an obvious, restrictive system) or an intricate system maintained all year through reproductive and non-reproductive periods.

The salt-marsh harvest mouse (*Reithrodontomys raviventris raviventris*) represents an example of a non-regimented system (Fisler, 1965). This form, in the laboratory, exhibits little aggression or site attachment. Only pregnant females build nests and then very weakly. There appears to be no real defense of the nest. In the field, the same tendencies are evident (Fisler, 1965, and unpublished). Whether in breeding season or not, these mice are highly mutually tolerant of each other. Apparently under environmental conditions of dense cover and frequent tidal inundation of their habitat, it is difficult to establish a home site and thus it is disadvantageous for this species to develop (or retain) great site attachment tendencies. Therefore, development of breeding aggregations or territories would likewise be inadapative. Rather, the most effective way to insure survival under the peculiar marsh conditions was high toleration, freedom of movement of individuals, no close relationships between adult individuals (copulation only), and little necessity for parental care (young are self-sufficient in three or four weeks). The only social attachment is the brief mother-young relationship.

On the other hand, a closely related upland species (presumably the ancestor of the marsh form), the western harvest mouse (*R. megalotis*), without tidal effects and with sparse cover, is a more excitable, aggressive animal which does socially organize into male territories with one male dominant over any other in the immediate vicinity (Fisler, 1965). Nests are well-built and defended. But such organization is found only in breeding individuals, for when non-breeding these mice are mutually tolerant. A reproductive hierarchical spatial territory (see beyond) is possible because the habitat has not im-

posed restrictions of a nature that prevent this more intimate organization.

A second example can be drawn from the work of Darling (1937) on the red deer (*Cervus elephas*). In the non-breeding season, matriarchal herds composed of females, fawns, and immatures of both sexes are formed. Adult males are solitary or form small, loose, wide-ranging herds. Male and female herd ranges may overlap, but not those of females, nor those of males. The matriarchal herd occupies a group undefended home range (see beyond), and the organization within each group is hierarchical. The male herds are not specifically organized. Why? Female herds contain the young which must be defended, and lacking organization, defense would be individualistic or non-existent, with perhaps each female defending only her own young. A group defense is more effective. Selectively, the male herds do not require communal protection, as the loss of a few individuals is not important. Each male essentially fends for himself, deriving what minimal protection he can obtain from the loose aggregate with which he may associate. Also, groups probably tend to compete more successfully for choice land than do individuals. Female herds require better forage for proper development of the young, and stronger organization within each herd is dictated to maintain a sufficient area. Competition among male herds is nil, as enough suitable males will survive for breeding under most conditions. Familiarity with one area seems to be desirable for coordinated defense or flight and this can be accomplished better through group attachment to a particular site.

A further question arises as to why adult males and females do not exist in the same herds during the non-breeding season. Would it not be more efficient for males to defend the herd instead of, or as well as, females? Again, the answer to this apparently lies in other proximate factors impinging upon the formation of the organizational system. There may be some niche separation between the two types of herds. Male herds may occupy less desirable areas, and it may be advantageous for the species to "weed out" those males that are unnecessary (extra) so that they do not compete directly for food with fawns and females. No matter what the reason(s) may be, the fact remains that these herds are separated during most of the year (10 months) and only during the reproductive period do we find establishment of a different system designed to facilitate the breeding of the stronger individuals, that is, an organizational system in which the more dominant males control the most females in harems. A shifting arena defensarium (see beyond) is formed and maintained. However, within the group (harem), there still exists a female hierarchy and a female still leads the group (including the male). The basic female herd structure still exists, although a reproductive type of organizational system of only two months duration has been superimposed on the usual type.

A third example can be taken from the primates. The social organization of many baboons, macaques, and others, has recently been well-reported (e.g., see Southwick, 1963; DeVore, 1965). In the rhesus macaque (*Macaca*

mulatta), bands are composed all year of all age and sex groups. The dominant males form a linear hierarchy, as do the females, although the latter hierarchy is not as clear, nor is the relationship between the two hierarchies clear. The young may assume hierarchical status as adults dependent somewhat on the status of the female parent (Koford, 1963a). In short, the band remains more or less constant in content and individual status throughout the year. Previously (Zuckerman, 1932, and others), it had been considered that bands of primates were held together because of year around sexual attraction. Yet recent work indicates that many, if not most, primates do have breeding seasons (Lancaster and Lee, 1965), just as do most other mammals. It becomes clear, then, that sex is not the only factor responsible for keeping the organizational system intact (Lancaster and Lee, 1965). There must be factors other than sex of more importance through the entire year which make a year around, relatively stable system advantageous. Apparently, any change of the basic system in the primate band for reproductive purposes is not advantageous, as indicated by the fact that there are no other systems superimposed.

The most obvious reason for a continuing organizational system such as exhibited by the rhesus bands would be the necessity for the care and defense of the young. These are relatively dependent on the adult female for two or three years, a period of time longer than in most mammals. Thus long-term female groups, as in the red deer, are necessary. But why are the males also in the group? Why are there not male groups, as in the red deer? Firstly, food may not be a factor requiring separation. Most primates live in tropical or semi-tropical areas without harsh winters (droughts or dry seasons, however, may impose harsh food conditions). Males may not be a burden on the band when they select the best foods for themselves. Secondly, males do function in defense of the band, especially in the defense of the young. This is apparently of greater selective value than having only subadult males and adult females performing this task. The subadult male may be inadequate in defense, the adult female less effective and hampered by the presence of a relatively immobile and helpless youngster. The latter is not true for the deer, where the young are mobile and less dependent on the female. Since the young rhesus are dependent for long periods, there is no time of the year when the males are not required for defense. A system developed thereby where all sex and age groups remain together all year, eliminating the development of a separate system for the breeding season. Orderliness and selection of the fitter males for breeding was provided for in the development of the hierarchy system in use at all times.

Inter-group relations

Monkey bands exhibit a certain degree of organization between and among each other. In the rhesus, some bands are dominant over others and may move relatively freely over the area occupied by another group. There may be various organizational aspects of *groups* which are similar to and parallel with organizations based on individuals. These inter-group relation-

ships vary with the primate species under consideration and many of them are well described in the papers found in DeVore (1965). Suffice it to say that development of these inter-group relationships in any mammal taxon is also dependent on the ultimate and proximate causes of organizational system development. The effect is presumably through the effect of individuals, however, rather than due to group selection (Wynne-Edwards, 1962).

Summary

The mouse, *Reithrodontomys raviventris*, is small, inconspicuous, and a prey species. Its organizational system is greatly influenced by these factors in addition to sex and habitat. The red deer is a large, conspicuous, prey species. Its size allows a greater freedom of movement; it now has few, if any, predators. (Its North American counterpart, *Cervus canadensis*, has the same type of organizational system, and predators (Murie, 1951)). It cannot be as inconspicuous as the mouse; an aggregating type of organizational system is allowable, as aggregations will not greatly change its relation to predator species through increased probability of attack. The predator could find it easily anyway, even if not grouped. The ease of finding the group over the individual has no effect, as group defense makes up for this shortcoming. A mouse aggregation would only destroy the advantage an individual has of being inconspicuous. The rhesus monkey is of intermediate size and conspicuousness, and its organizational system is complicated by the relative helplessness of the young and the length of time required to raise them. The monkey is large enough so that aggregations are not sufficiently disadvantageous to preclude development of sociality. Food habits are not restricting so as to separate bands by sex. Defense and the long dependence of the young favor a system with the greatest amount of predator defense. Sociality and other advantages of this organization occurred after or with the initial evolution of the group system, not prior to the development of such a system. It should be noted further that only the largest primates, those in least danger from predators, have developed highly flexible and even non-hierarchical or non-territorial group systems (chimpanzee, *Pan troglodytes*; gorilla, *Gorilla gorilla*; see Table 11).

Conclusions

From the above discussion, it is apparent that studies of organizational systems of mammals require extremely detailed data on ecology and social relations if one is to discern the origin and development of each system and all its ramifications for individual species. Careful attention to details of organization at all times of the year is necessary. In compiling the tables in this paper, many good studies could not be used because of the lack of detailed information. Eisenberg (1965) has previously stressed this fact and has listed many relationships which should be studied.

Furthermore, the organizational system evolved may change as the proxi-

mate factors fluctuate. It would be adaptive for a population to utilize different or slightly differing systems under changing environmental conditions. These major or minor system changes through fluctuations of proximate factors result in the myriad shades of differences that one encounters in the study of mammalian organizational systems. Dynamic, flexible, adaptive systems such as these defy classification in the classical sense of "any defended area," and also defy relegation to a simple hierarchical system of a static nature. The system of classification used by Eisenberg (1965), while very useful and probably correct in the main, does not provide any practical system for succinct discussion of spatial and social relationships. The discussion by Calhoun (1963), pointing out possible factors involved in the social use of space, particularly with regard to group size, does not furnish a classification in a practical sense.

A CLASSIFICATION OF MAMMALIAN ORGANIZATIONAL SYSTEMS

An organizational system in the context of this paper refers to any type of organization that is present in any species. By definition, then, all species have such a system even though this is not always "social" in the normal context of frequent interaction between and among individuals. Solitary species have their own particular system, even as do highly "socialized" group and colonial species. In other words, a system in this paper goes beyond the relations of individuals in close proximity, even beyond the transitory relations of a pair of mammals in copulation, or the mother-young relationship, which may be the only sociality (in the usual sense) of some species. These systems represent the manner in which species are organized in space and behavior at any particular time of the year or sexual cycle.

Organizational systems cannot be viewed from a static concept in which one species is considered territorial, another occupies a core area, and a third species is hierarchical. They are flexible, dynamic systems of adjustment of the populations to the organization that is best adapted to the major proximate factors, perhaps even working to the detriment of some factors if the overall adaptation to the environment is favorable. Therefore, many species will have different types of organizational systems through the course of the annual cycle. For example, it is misleading to speak of a species of deer as being harem-forming unless this is displayed all year. De Vos, *et al.*, (1967) have recently reviewed the social behavior of North American cervids during the reproductive period and have clearly pointed out the differing social organizations through the yearly cycle. Leuthold (1966) has discussed the variations and evolution of the types of territorial systems in the Uganda kob (*Adenota kob*), pointing out various factors (proximate) affecting the organizational structure under differing behavioral and environmental conditions. One must distinguish between the differing organizational systems throughout the year for any species of mammal studied.

As in many classifications, the distinctions between categories here are not always discrete. Indeed, in dynamic systems this cannot be so. For example, a

mammal holding a classic spatial territory (Table 1) is in all likelihood also holding a nidic territory (Table 2). In placing species in their categories, I have tried to place them in the category which seems spatially broadest, even though they may also fit another, less encompassing territorial class. So even though a mammal species may hold a permanent nidic territory, if the broader organization shows a basic exclusive core monopolization, it will be so classified. Investigators should spell these details out in their studies.

A further problem is that of the concept of home range. The classic definition of Burt (1943), essentially area traversed in day to day activities, though not necessarily defended, is still acceptable. It is apparent now that most species of mammals do have home ranges, preferred areas of occupancy. Very few species are truly nomadic, traversing any area without regard to particular sites but remaining only in the proper habitat. All species in this classification do have preferred areas, but these may shift from time to time. The utilization of this home range by the individual, and any shifting of the area occupied, depend on the ultimate and proximate factors listed earlier in this paper, with site attachment being the primary reason for the existence of the home range. How an individual within a mammalian species uses this home range in relation to space and other individuals, whether this individual defends all of the home range, a part of it, or none of it, is part of the organizational system of that species.

Lastly, the concept that has been termed individual distance (Hediger, 1950), or personal space (Marler and Hamilton, 1966), must be considered. The former term was introduced for interspecific reactions but could also be used on an intraspecific basis. Hediger's terms, and several additional similar terms, have recently been discussed by Hall (1966). There is a greater or lesser distance around many mammals within which they ordinarily will not allow the approach of another individual. This characteristic seems to be responsible for the formation of organizational systems called here "personal space dispersion" and "group psychic space." Although many species, if not most, have a personal, probably defended, space (or self), this does not usually supersede other orders of organization. At times, it may be difficult to separate personal space (a behavioral concept) from a spatial concept. For example, an individual defending only a single homesite (permanent nidic territory) may be defending just that, space, or it may be defending only itself, located within the homesite. One certainly gains the impression that a species which defends a changing homesite (shifting nidic territory) may well be defending only itself, its personal space, with no real spatial connotations. Only further detailed study will resolve this situation. A "group psychic space" involves defense of the group and its current location without reference to fixed spatial boundaries, thus extending the concept beyond the individual alone.

The classification proposed here does not pretend to be complete and definitive. Probably no such classification can be. However, it is hoped that this grouping (1) will serve as a guideline and can be modified as our rather incom-

plete knowledge of these systems is amplified with new work, and (2) will place emphasis on the dynamism of organizational systems. I have tried to use terms currently in use rather than invent new ones, although at times certain classical definitions may be modified. Certain new terms were also found necessary. Some species may not fit precisely into the categories as outlined here. This is to be expected in a dynamic system. Furthermore, many species will be listed under several categories, reflecting changes of systems over yearly and sexual cycles. Also, a few species placed in one category at this time may have to be moved to another as new data dictate. Our knowledge of the details, and even generalities, of social behavior is still imperfect (Eisenberg, 1965).

This system of classification has one basic dichotomy; organizational systems based on the individual, and organizational systems based on the group. I have made no attempt to categorize by age groups, and the dichotomy here is based on adult systems. Individual organization of a species occurs when the primary structure rests with the activities and actions of single individuals, or all individuals are allowed independent action with essentially no dependence on group action. Group organization occurs when the primary organizational structure of the species depends on the concerted efforts of more than one individual so that the group may act as an integrated whole and may take on properties of the individual (see Eisenberg, 1965, for a further elucidation of grouped versus aggregated individuals). Many species exhibit more than one type of organization, frequently at the same time. Examples will be found in Tables 1 through 11, and there is a detailed example for one species given in the legend for Figure 1.

I. Organizational systems based on individuals:

- A. Spatial territory (Table 1); defense of a given plot of ground within, or even including the entire, home range.
 - 1. Exclusive—defense of an area excluding all conspecifics. Only exception is a brief period for breeding. May be a shifting area.
 - 2. Classic—area permanently defended from conspecifics of the same sex.
 - 3. Shifting classic—as in IA2 except that area defended may change over time. With further evidence, it is quite likely that IA2 species may belong in this category. Includes slight alterations to major shifts and movement to a completely new area.
 - 4. Hierarchical—defense of an area including several individuals (of both sexes) but with one animal (male) dominant. Remainder defend sub-territories but are inferior to the dominant who has access to all the territory.
- B. Nidic territory (Table 2); defense of the nest or homesite only (probably primarily restricted to females, particularly perinatal individuals).
 - 1. Permanent—defense of a permanent nest or homesite.
 - 2. Shifting—defense of the nest(s) or homesite(s) currently used by the individual.

- C. Arena territory (Table 3); defense of a specific plot of ground for copulation or harem formation, or both. Restricted mostly to males as a special reproductive system.
1. Individual—defense of an area (usually small) by an individual which allows females to enter, but individual females do not remain.
 2. Haremic—defense of an area (usually large) which females occupy relatively permanently.
- D. Shifting arena defensarium (Table 4); defense of living animals which move about, therefore not defense of a specific plot of ground. Restricted mostly to males.
1. Haremic—defense of the harem, or the space which the harem currently occupies.
 2. Individual—defense of the individual, or the space which the individual currently occupies.
- E. Core monopolization; no overt defense of a plot of ground but use of an area of concentrated activity within the larger range of the individual. Many species probably exhibit this system but data as yet are not clear. Further work should provide definitive examples for this category.
1. Trespass—occasional conspecific intrusion.
 2. Exclusive (monopolized area of Jewell, 1966)—no conspecific intrusion.
- F. Personal space dispersion (Table 5); includes essentially solitary species where avoidance of conspecifics is the rule; thus individuals are dispersed although they may move over the same ground. This is conspecific personal space at its greatest development. It may also include some aggregating forms where no other form of organizational system is utilized. Many species here are not overtly hostile to conspecifics (little overt aggression) but may exhibit some site attachment.
1. Solitary—individuals that live alone most of their lives.
 2. Aggregate—individuals that aggregate or live in close proximity to one another.
- G. Hierarchy (Table 6); individuals involved with diminishing rights of "possession" within a group; therefore associated with groups of individuals. Hierarchies, requiring two or more individuals, are a result of decreased aggression, increased sociality, lessened individual site attachment, that is, increased group attachment. As such, this class forms a transition between individual and group systems and has characteristics of both individual and group organizations.
1. Linear—a straight line hierarchy where A is dominant over B, B over C, etc. It may be a rigid system or a more flexible system of dominance by frequency rather than absolute right.
 2. Overlapping—a system where A is dominant over B, B over C, but C over A, etc.

3. Ruling consortium—several of the highest ranking individuals support one another in domination of the other individuals.
 - H. Undefended home range (Table 7); use of all areas freely by all individuals. No aggression apparent but there may be some preference for certain areas by individuals. Mostly aggregates.
- II. Organizational systems based on groups:
- A. Spatial territory (Table 8); group defense of a plot of ground. Contains all of the subtypes listed under individual spatial territory.
 - B. Core monopolization (Table 9); as in individual core monopolization including both subtypes.
 - C. Group psychic ("personal") space; defense of the area which the group currently occupies rather than a permanent plot of ground. A "moving territory." Group composed of all ages and both sexes. Example, howler monkey (*Alouatta palliata*), Carpenter, 1965, possibly.
 - D. Hierarchy (Table 10); groups maintain levels of dominance among one another.
 1. Linear—a straight line hierarchy as in individual hierarchies.
 2. Overlapping—dominance dependent more on circumstances than upon dominance rights of one group over another.
 - E. Undefended home range (Table 11); no apparent aggression between groups.

The preceding categorization, as emphasized earlier, is based on site attachment and aggression. Through this classification of organizational systems there is a decrease in individual aggression from IA through IH and continuing on into group structure, the latter made possible by decreasing individual aggression. Also, within group organization, there is a decrease in group aggression from IIA through IIE. Similarly, there is a decrease in spatial attachment from IA through IG and from IIA through IID. Spatial attachment in IH and IIE may be present but is not of over-riding importance in the organizational structure. A graphic summary of the organizational systems and factors involved in their formation is presented in Figure 1.

There is some question whether IB (nidic territory) is really a part of IA (spatial territory). Since, however, it is such a specialized interaction (or the original territorial condition?) involving defense of nest or den alone, it deserves separate rank and importance. Many female mammals may exhibit only this type of organization, hence it should be recognized on this basis alone.

A further problem concerns the type of relationship involved with a female in defense of her young. Certainly this is a part of any organizational system. However, since this appears to be such a universal mammalian characteristic, this relationship probably is simply an extension of categories already listed, such as nidic, or an extension of the personal space of the female to include the young.

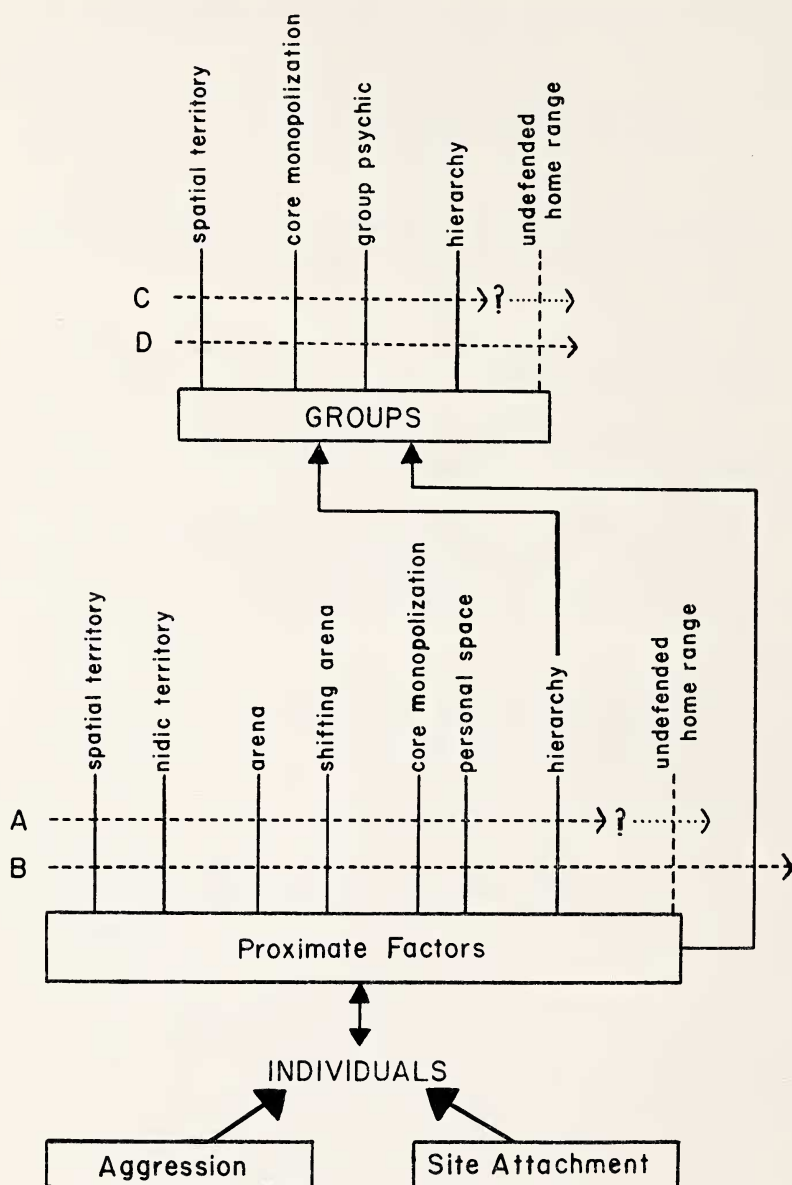


Figure 1. Inter-relationships of mammalian organizational systems and factors determining these systems. Horizontal distance between vertical lines to the organizational systems indicates degree of relationship between systems. Additional organizational

In selecting examples for the tables, I have chosen those which, on current data, illustrate the principles involved. Further references may be found in Eisenberg (1965). In essence, this classification recognizes the fact (which has been recognized by earlier authors) that hierarchy and territory are different ways of solving adjustment of populations to their environment, abiotic and biotic, but having the same base. I hope that it will provide a basis for recognition of the fact that most mammals do not fit into one convenient definition of territory, but, rather, either this term must provide considerably more latitude, or new terms must be coined for the varying systems of organization. By perusing the literature, it is evident that we no longer can abide by the concepts as they were first applied to mammals, useful as these were at that time. Indeed, perhaps a closer look should be taken at classic definitions of territory and hierarchy in other vertebrate groups, particularly birds, as there are dominance orders related to the territory occupied (discussed in Colquhoun, 1942; Brown, 1963, 1964; Willis, 1967).

The organizational system developed by any mammalian species depends on many factors and not necessarily on its phylogenetic history. The only phylogenetic trends through the order Mammalia for which there is evidence are (1) that those mammals with seemingly more complex brains tend toward group organizational systems (primates and ungulates), and (2) that there is a general size increase from the smaller species holding spatial territories to the larger species holding other, succeeding systems (as outlined in this paper). Since early studies concerned mostly small mammals, perhaps this accounts for the over-emphasis on territory as a spatial concept only.

In conclusion, in order to discuss organizational systems with understanding and meaningfulness, and in order to make valid comparisons, we are now in need of a system which will provide a basis for realization of the intricate balance set up between spatial and behavioral conditions, and that ultimate and proximate factors as outlined previously in this paper are responsible for the current form of any mammalian organizational system.

types may be added as data warrant. A = decreasing individual site attachment. B = decreasing individual overt aggression. C = decreasing group site attachment. D = decreasing group overt aggression.

The position of the category "undefended home range" is unsure. Degree of site attachment is also uncertain for this category. Also, it should be kept in mind that any species can exhibit more than one organizational type through the year, and that different sex and age groups frequently have different organization. Any change in the proximate factors may also effect a change in the organizational type. For example, female red deer (*Cervus elephas*) exhibit an undefended home range throughout the year; males are similar (but separate) during the non-breeding stages, but some change to a shifting arena defensarium during breeding.

TABLE 1
Some mammalian species exhibiting a spatial territory (type IA). Subtypes are 1, exclusive; 2, classic; 3, shifting classic; 4, hierarchical. Explanations may be found in the text. B = breeding, N = nonbreeding.

Species	Subtype	Sex	Season	Other types	Authority
MARSUPIALIA					
<i>Isodon obesulus</i>	2 or 3	♂, ♀	B, N	None	Heinsohn, 1966
<i>Trichosurus vulpecula</i>	2, 4 (occasionally)	♂	B, N	IH	Dunnet, 1964
INSECTIVORA					
<i>Sorex araneus</i>	1	♂, ♀	B, N	None	Crowcroft, 1957
LAGOMORPHA					
<i>Ochotona princeps</i>	1-2	?	?	None	Kilham, 1958; Broadbooks, 1965
<i>Oryctolagus cuniculus</i>	4	♂, ♀	B, N (reduced)	None	Lockley, 1961
RODENTIA					
<i>Marmota monax</i>	4	♂, ♀	N, B (probably)	None	Bronson, 1964
<i>Spermophilus beecheyi</i>	2	♂	B, N	IB	Evans and Holdenried, 1943
<i>Tamias striatus</i>	2	♀	B	?	Yerger, 1953
<i>Tamiasciurus douglasi</i>	2	?	?	?	Gordon, 1936
<i>Thomomys bottae mewa</i>	1	♂, ♀	N	None	Howard and Childs, 1959
<i>Peromyscus crinitus</i>	2?	♂	B	IB, IH	Eisenberg, 1963a
<i>Peromyscus leucopus</i>	2?	♂	B	IB, IH	Nicholson, 1941
<i>Peromyscus maniculatus</i>	2?	♂, ♀?	B	IH	Howard, 1949
<i>Reithrodontomys megalotis</i>	4	♂	B	IB, IH	Fisler, 1965
<i>Apodemus sylvaticus</i>	4	♂, ♀?	B	?	Brown, 1966
<i>Mus musculus</i>	4	♂, ♀	B, N	?	Crowcroft, 1955; Reimer and Petras, 1967
<i>Ctenomys optimus</i>	1	♂, ♀	B, N	None	Pearson, 1959
<i>Ctenomys peruanus</i>	?	♂	B, N	IH	Pearson, 1959
CARNIVORA					
<i>Mustela erminea</i>	2	♂, ♀	B, N	None	Lockie, 1966
<i>Mustela nivalis</i>	2	♂, ♀	B, N	None	Lockie, 1966

TABLE 2
Some mammalian species exhibiting a nidic territory (type IB). Subtypes are 1, permanent;
2, shifting. Explanations may be found in the text. B = breeding, N = nonbreeding.

Species	Subtype	Sex	Season	Other types	Authority
MARSUPIALIA					
<i>Perameles gunni</i>	2 (may be hierarchical)	♂, ♀	B, N	None	Heinsohn, 1966
RODENTIA					
<i>Spermophilus beecheyi</i>	2?	♀	B, N	IA	Linsdale, 1946
<i>Tamiasciurus hudsonicus</i>	?	♂, ♀	B, N	None?	Layne, 1954
Heteromyidae	?	♂, ♀	B, N	None	Eisenberg, 1963b
<i>Peromyscus crinitus</i>	1?	♀	B	IA, IH	Eisenberg, 1963a
<i>Peromyscus leucopus</i>	1?	♀	B	IA, IH	Nicholson, 1941
<i>Reithrodontomys megalotis</i>	2	♀	B	IA, IH	Fisler, 1965
<i>Myocastor coypus</i>	1?	♂, ♀	B, N	IF	Ryszkowski, 1966

TABLE 3

Some mammalian species exhibiting an arena territory (type IC). Subtypes are 1, individual; 2, harem. Explanations may be found in the text. B = breeding, N = nonbreeding.

Species	Subtype	Sex	Season	Other types	Authority
CHIROPTERA					
<i>Pteropus poliocephalus</i>	2	♂, ♀	B (summer)	IF, IH	Nelson, 1965
PINNIPEDIA					
<i>Zalophus californianus</i>	2	♂	B	?	Orr, 1967
<i>Zalophus wolfebaeki</i>	2	♂	B	?	Orr, 1967
<i>Callorhinus ursinus</i>	2	♂	B	IH	Bartholomew and Hoel, 1953
<i>Halichoerus grypus</i> Western Atlantic	2	♂	B	?	Cameron, 1967
<i>Halichoerus grypus</i> Eastern Atlantic	1	♂	B	?	Darling, 1947
HYRACOIDEA					
<i>Procavia johnstoni</i>	2	♂	B, N	?	Coe, 1962
ARTIODACTYLA					
<i>Lama vicugna</i>	2	♂	B, N	IH	Koford, 1957
<i>Connochaetes taurinus</i>	1	♂	All year	?	Estes, 1966
<i>Adenota kob thomasi</i>	1	♂	All year	IIE	Buechner, 1961; Leuthold, 1966
<i>Kobus leche</i>	2	♂	B	IIE?	de Vos and Dowsett, 1966
<i>Kobus vardonii</i>	2	♂	B	IIE?	de Vos and Dowsett, 1966
<i>Gazella granti</i>	1	♂	B	IIE?	Dowsett, 1966
<i>Gazella thomsonii</i>	1	♂	B	IIE?	Estes, 1967

TABLE 4

Some mammalian species exhibiting a shifting arena defensarium (type ID). Subtypes are 1, harem; 2, individual. Explanations may be found in the text. B = breeding, N = nonbreeding.

Species	Subtype	Sex	Season	Other types	Authority
PRIMATES					
<i>Erythrocebus patas</i>	1	♂ + ♀ ♀	B, N	IIA	Hall, 1965
<i>Papio hamadryas</i>	1	♂ + ♀ ♀	B, N	IID	Kummer and Kurt, 1963
<i>Theropithecus gelada</i>	1	♂ + ♀ ♀	B, N	IIB	Crook, 1966
PERISSODACTYLA					
<i>Equus caballus przewalskii</i>	1	♂ + ♀ ♀	B, N	?	Bannikov, 1958
ARTIODACTYLA					
<i>Cervus elephas</i>	1	♂ + ♀ ♀	B	IH, IIE	Darling, 1937; Lowe, 1966
<i>Rangifer tarandus groenlandicus</i>	2?	♂ + ♀	B	IH	Lent, 1965

TABLE 5

Some mammalian species exhibiting personal space dispersion (type IF). Subtypes are 1, solitary; 2, aggregate. Explanations may be found in the text. B = breeding, N = non-breeding.

Species	Subtype	Sex	Season	Other types	Authority
MONOTREMATA					
<i>Tachyglossus aculeatus</i>	1	♂, ♀	B, N	None?	Hediger and Kummer, 1961
MARSUPIALIA					
<i>Didelphis marsupialis</i>	1	♂, ♀	B, N	None?	Lay, 1942
CHIROPTERA					
<i>Pteropus poliocephalus</i>	2	♂, ♀	B, N	IC, IH	Nelson, 1965
<i>Pteropus scapulatus</i>	2	♂, ♀	B, N	IC, IH	Nelson, 1965
EDENTATA					
<i>Myrmecophaga tridactyla</i>	1 (nomadic?)	♀, ♂?	B, N	None?	Krieg and Rahm, 1961
RODENTIA					
<i>Spermophilus armatus</i>	2	♂, ♀	B, N	None	Balph and Stokes, 1963
<i>Myocastor coypus</i>	2	♂, ♀	B, N	IB	Ryszkowski, 1966
CARNIVORA					
<i>Nasua narica</i>	1	♂	N	IIB	Kaufmann, 1962
TUBULIDENTATA					
<i>Orycteropus afer</i>	1	♀, ♂?	B, N	None?	Rahm, 1961

TABLE 6

Some mammalian species exhibiting a hierarchy system (type IG). Subtypes are 1, linear; 2, overlapping; 3, ruling consortium. Explanations may be found in the text. B = breeding, N = nonbreeding.

Species	Subtype	Sex	Season	Other types	Authority
PRIMATES					
<i>Macaca mulatta</i>	1, 3	♂, ♀	B, N	IID	Koford, 1963b
<i>Papio anubis</i>	1, 3	♂, ♀	B, N	IIB	Hall and DeVore, 1965
<i>Papio ursinus</i>	1, 3	♂, ♀	B, N	IIB	Hall and DeVore, 1965
<i>Colobus quenza</i>	1?	♂, ♀	B, N	IIA	Ullrich, 1961
<i>Presbytis entellus</i>	1, 3?	♂, ♀	B, N	IIB	Jay, 1965
<i>Gorilla gorilla beringei</i>	1	♂	B, N	IIE	Schaller, 1963
RODENTIA					
<i>Cynomys ludovicianus</i>	1	♂	B, N	IIA, IIB	King, 1955
<i>Tamias striatus</i>	1	♂, ♀	B, N?	None	Wolfe, 1966
PROBOSCIDEA					
<i>Elephas indicus</i>	1?	♂, ♀?	B, N	?	Deraniyagala, 1955

TABLE 7
Some mammalian species exhibiting individual undefended home ranges (type IH).
B = breeding, N = nonbreeding.

Species	Sex	Season	Other types	Authority
MARSUPIALIA				
<i>Trichosurus vulpecula</i>	♀	B, N	IA	Dunnet, 1964
<i>Macropus canguru</i>	♂, ♀	B, N?	None	Caughley, 1964
<i>Macropus rufus</i>	♂, ♀	B, N?	None	Caughley, 1964
CHIROPTERA				
<i>Pteropus poliocephalus</i>	♂, ♀	N (winter)	IC, IF	Nelson, 1965
<i>Pteropus scapulatus</i>	♂, ♀	N (winter)	IC, IF	Nelson, 1965
<i>Rousettus aegyptiacus</i>	♂ + ♀	All year	None	Kulzer, 1961
RODENTIA				
<i>Peromyscus crinitus</i>	♂, ♀?	N	IA, IB	Eisenberg, 1963a
<i>Peromyscus leucopus</i>	♂, ♀	N	IA, IB	Nicholson, 1941
<i>Peromyscus maniculatus</i>	♂, ♀	N	IA	Howard, 1949
<i>Reithrodontomys megalotis</i>	♂, ♀	N	IA, IB	Fisler, 1965
<i>Reithrodontomys raviventris</i>	♂, ♀	B, N	None	Fisler, 1965
<i>Ctenomys peruanus</i>	♀	B, N	IA	Pearson, 1959
PINNIPEDIA				
<i>Callorhinus ursinus</i>	♀	B, N?	IC	Bartholomew, 1953
ARTIODACTYLA				
<i>Lama vicugna</i>	♂ (bands)	B, N	IC	Koford, 1957
<i>Cervus elephas</i>	♂	N	ID, IIE	Darling, 1937; Lowe, 1966
<i>Rangifer tarandus groenlandicus</i>	♂, ♀	B, N	ID, IIE?	Lent, 1965
<i>Giraffa camelopardalis</i>	♂, ♀	All year	IIE?	Innis, 1958
<i>Ovis aries</i> (feral)	♂	B	IIB	Grubb and Jewell, 1966
<i>Ovis canadensis</i>	♂	B	IIB	Buechner, 1960

TABLE 8

Some mammalian species exhibiting group spatial territory (type IIA). Subtypes are 1, exclusive; 2, classic; 3, shifting classic; 4, hierarchical. Explanations may be found in the text. B = breeding, N = nonbreeding.

Species	Subtype	Sex	Season	Other types	Authority
PRIMATES					
<i>Erythrocebus patas</i>	2	♂ + ♀	B, N	ID	Hall, 1965
<i>Colobus quersa</i>	2	♂ + ♀	B, N	IG	Ullrich, 1961
<i>Hylobates lar</i>	2?	♂ + ♀	B, N	None?	Carpenter, 1940
RODENTIA					
<i>Cynomys ludovicianus</i>	1	♂ + ♀ (coterie)	B, N	IG, IIB	King, 1955
<i>Castor canadensis</i>	2	♂ + ♀	B, N	None	Bradt, 1938
CARNIVORA					
<i>Panthera leo</i>	2	♂ (♂) + ♀ ♀	B, N	None	Schenkel, 1966

TABLE 9
Some mammalian species exhibiting group core monopolization (type IIB). Subtypes are 1, trespass; 2, exclusive. Explanations may be found in the text. B = breeding, N = nonbreeding.

Species	Subtype	Sex	Season	Other types	Authority
PRIMATES					
<i>Papio anubis</i>	1	♂, ♀	B, N	IG	DeVore and Hall, 1965
<i>Papio ursinus</i>	1	♂, ♀	B, N	IG	DeVore and Hall, 1965
<i>Theropithecus gelada</i>	1	♂, ♀	B, N	ID	Crook, 1966
<i>Presbytis entellus</i>	2	♂, ♀	B, N	IG	Jay, 1965
RODENTIA					
<i>Cynomys ludovicianus</i>	1 (ward, town)	♂, ♀	B, N	IG, IIA	King, 1955
CARNIVORA					
<i>Nasua narica</i>	2	♀ ♀	B, N	IF	Kaufmann, 1962
ARTIODACTYLA					
<i>Ovis aries</i> (feral)	2	♀	B, N	IH	Grubb and Jewell, 1966
	2	♂	N	IH	Grubb and Jewell, 1966
<i>Ovis canadensis</i>	1	♀	B, N	IH	Buechner, 1960

TABLE 10

Some mammalian species exhibiting group hierarchy (type IID). Subtypes are 1, linear; 2, overlapping. Explanations may be found in the text. B = breeding, N = nonbreeding.

Species	Subtype	Sex	Season	Other types	Authority
PRIMATES					
<i>Macaca mulatta</i>	1	♂ + ♀	B, N	IG	Koford, 1963b
<i>Papio hamadryas</i>	2	♂ + ♀	B, N	IE	Kummer and Kurt, 1963

TABLE 11

Some mammalian species exhibiting a group undefended home range (type IIE). B = breeding, N = nonbreeding.

Species	Sex	Season	Other types	Authority
PRIMATES				
<i>Pan troglodytes</i>	♂, ♀	B, N	None	Goodall, 1965; Reynolds and Reynolds, 1965
<i>Gorilla gorilla beringei</i>	♂, ♀	B, N	IG	Schaller, 1963
ARTIODACTYLA	♀	B, N	ID, IH	Darling, 1937; Lowe, 1966
<i>Cervus elephas</i>		B, N	IH	Innis, 1958
<i>Giraffa camelopardalis</i>	♂, ♀ (mixed herds)	All year	IC	Leuthold, 1966
<i>Adenota kob thomasi</i>	♂ bachelor herds ♀ herds	All year		

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SUMMARY

The concepts of territory and hierarchy should be considered as opposite extremes of a continuum of organizational systems of mammals. These systems are the result of two fundamental characteristics, aggression and site attachment (ultimate factors), which are acted upon additionally (at the individual level) by proximate factors such as basic morphology, levels of aggression and site attachment, habitat occupied, interspecific populational effects, competition of various types, population density, and climate. Examples of how the ultimate and proximate factors impinge upon and adapt a population to its environment are given.

A classification for mammalian organizational systems utilizing a basic dichotomy of individual and grouped organizations subdivided into spatial territory, nidic territory, arena territory, shifting arena defensarium, core monopolization, personal and group space dispersion, hierarchy, and undefended home range, is suggested. Data for support of this system are given. No phylogenetic trends were evident within this system other than that those species with seemingly more complex brains tend toward group organization, and smaller species tend to be found at the territorial end of the organizational system spectrum. It is hoped that this system will help clarify evident confusion as to the relationships among mammalian organizational systems.

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